

ELYMUS STEBBINSII: TAXONOMY, NOMENCLATURE, AND DISTRIBUTION

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ABSTRACT

Elymus stebbinsii was originally named *Agropyron parishii* by Scribner & Smith, who recognized two varieties in it, *A. parishii* var. *parishii* and *A. parishii* var. *laeve*. Discovery that the holotype of var. *laeve* belongs in *E. trachycaulus* raised the question of whether there is a valid taxon corresponding to the description, but not the type, of var. *laeve*. Examination of specimens from several Californian herbaria, combined with phenetic analyses of morphological data, supports Scribner & Smith's recognition of a long-awned taxon within *E. stebbinsii* for which the name *E. stebbinsii* subsp. *septentrionalis* is proposed. This subspecies grows in the western Sierra Nevada and southern Cascade Mountains, whereas subsp. *stebbinsii* grows near the coast of northern California and in the Transverse Ranges. Herbarium records indicate that subsp. *septentrionalis* is the more abundant of the two taxa. The study also revealed that plants of *E. glaucus* may have anthers as long as 4.6 mm, a considerable increase over the previously reported upper limit of 3 mm. A key to the Californian species of *Elymus* is presented.

KEY WORDS: *Agropyron parishii*, *Agropyron parishii* var. *laeve*, *Elymus stebbinsii*, California, North America, taxonomy, nomenclature, Hordeaceae, Triticeae, Poaceae

NOMENCLATURAL HISTORY

The basionym of *Elymus stebbinsii* Gould is *Agropyron parishii* Scribner & J.G. Sm., a species the authors (Scribner & Smith 1897) described as differing from other species then included in *Agropyron* by its pubescent culm nodes and widely spaced, long-glumed spikelets. The species description was followed by the description of var. *laeve*: "[having] the habit of the species, but the culm nodes and leaf sheaths glabrous; awns as long or longer than the flowering glumes. Type in the Gray Herbarium No. 414, Dr. Edward Palmer, collected at Talleys [misread as Fowleys by

Scribner & Smith], Cuamaca [= Cuyamaca] Mountains, in the southern part of San Diego County, Cal., 1875". Table 1 summarizes the subsequent nomenclatural history of the two taxa.

Hitchcock (1912) raised var. *laeve* to a species as *Agropyron laeve*, but subsequently accepted Scribner & Smith's treatment of the two taxa (Hitchcock 1935, 1951), as did Munz (1959). Abrams (1940) treated both taxa as species. Gould (1947) was the first taxonomist to place the two varieties in *Elymus* L., but he also placed them in different species. He named transferred *Agropyron parishii* as *Elymus stebbinsii*, the combination *Elymus parishii* having been used earlier for another taxon (Hall 1902), but placed *A. parishii* var. *laeve* in *E. pauciflorus* (Schwein.) Gould as subsp. *laevis* (Scribner & J.G. Sm.) Gould. At the time, Gould thought that *Elymus pauciflorus* was the correct name for what had, until then, been known as *Agropyron trachycaulum* (Link) Malte, but Lamarck (1791) had already used it for another species. Shinnars (1954) corrected Gould's oversight, publishing the combination *E. trachycaulus* (Link) Gould ex Shinnars for *A. trachycaulum*, but did not publish a combination for *A. parishii* var. *laeve*. Thus, *A. parishii* var. *laeve* was left with no valid name in *Elymus*.

Gould gave no reason for changing the species to which var. *laeve* belonged, but it may have been as a result of examining the holotype. As Michael Curto pointed out (pers. comm., 1992), the holotype undoubtedly belongs in *Elymus trachycaulus*, having anthers about 2 mm long, whereas *Agropyron parishii* has anthers 3-6 mm long in addition to distant spikelets. The long awns of the holotype of var. *laeve* place it in *E. trachycaulus* subsp. *subsecundus* (Link) A. Löve & D. Löve.

Hoover (1966) agreed with Scribner & Smith that their *Agropyron parishii* included both unawned and awned plants, but did not consider that they merited separate recognition. He agreed with Gould, however, in placing the species in *Elymus*. Because Hoover combined *A. parishii* var. *laeve* with *A. laeve* var. *laeve* in a single species, he had to use *E. laevis* Hoover as its name, Hitchcock's (1912) publication of *A. laeve* giving that epithet priority over *stebbinsii* at the species level.

THE PROBLEM

The discovery that the holotype of *Agropyron parishii* var. *laeve* belongs in *Elymus trachycaulus* raised the question as to whether there is a long-awned variant of *A. parishii* that merits taxonomic recognition or whether all such plants belong to other taxa, the most likely candidates being *E. glaucus* or *E. trachycaulus* subsp. *subsecundus*.

Because UTC [herbarium codes from Holmgren *et al.* (1990)] has no specimens of *Agropyron parishii*, I borrowed specimens identified as *A. parishii*, *A. parishii* var. *laeve*, *Elymus stebbinsii*, or *E. laevis* from AHUC, CAS, CHSC, DAV, DS, JEPS, POM, RSA, and UC. I already had the holotype of *A. parishii* var. *parishii* on loan from US. Initial review of the specimens indicated that the problem was not simple. Many of the specimens borrowed belonged to *E. glaucus* or *E. trachycaulus*, but

identifying them on the basis of existing keys (including Barkworth 1993) proved frustrating.

Both *Elymus glaucus* and *E. trachycaulus* have been described as variable (Snyder 1950; Dreman 1995; Barkworth 1996), but there are few details about their variability in the literature. *Elymus glaucus* supposedly differs from both *E. trachycaulus* and *E. stebbinsii* having two spikelets per node, but plants with some or all of their spikes having one spikelet per node are not uncommon. It usually has more lax leaves, longer anthers, and glume veins that are more evenly scabridulous than *E. trachycaulus*, but the distinction between the two is not easy, particularly when working with herbarium specimens. It has been thought to differ from *E. stebbinsii* in having shorter anthers (1.5-3.0 mm vs. 3-6 mm; Barkworth 1993), but applying this range to identification of the loaned specimens made it evident that the upper limit needed revising.

Elymus trachycaulus supposedly differs from *Agropyron parishii* in its more imbricate spikelets and shorter anthers (0.8-2.5 mm vs. 3-6 mm). There are specimens of *E. trachycaulus* with distant spikelets, but the anther distinction is usually sufficiently consistent to be a reliable means of distinguishing between the two taxa if anthers are present. If they are not, the two taxa are hard to distinguish using existing keys.

After several unsatisfactory attempts to identify the specimens, I decided to conduct a morphometric study of the specimens. In addition to determining whether *Elymus stebbinsii* had infraspecific taxa that merited recognition, I hoped to find additional characters that, either singly or in combination with others, would make it easier to distinguish between *E. stebbinsii*, *E. glaucus*, and *E. trachycaulus*.

MATERIALS AND METHODS

The total number of specimens employed in this study was 168. Among them were the holotype and one isotype of *Agropyron parishii* var. *parishii* (US 556669 and DS 79635, respectively). I had examined the holotype of *A. parishii* var. *laeve* previously and, after convincing myself that it was *Elymus trachycaulus*, had returned it to GH. There were no isotypes of var. *laeve* among the specimens borrowed. I also requested a loan of the taxa from SD, but all the specimens that had at one time been placed in *A. parishii* or *E. stebbinsii* had since been annotated as belonging to other taxa, primarily *E. trachycaulus*. These were made available to me shortly after I had completed the major part of this study. I examined each specimen but found none that belonged in *E. stebbinsii*; consequently, they are not included in the data presented here.

Nineteen characters were scored on 148 specimens (Table 2). The specimens scored included all the relatively complete specimens that seemed to belong in *Agropyron parishii* (including the holotype and isotype), plus several specimens that were puzzling, and others that I thought belonged in *Elymus glaucus*. For the numerical analyses, each specimen was considered to be a single Operational Taxonomic Unit (OTU) but, whenever feasible, inflorescence characters were

measured on the same culm as vegetative characters and spikelet characters were measured on a spikelet from the mid-region of the same inflorescence.

Table 1. Nomenclatural history of *Agropyron parishii* and *A. parishii* var. *laeve*. Names within a column are based on the same type specimen. The unshaded cells with names refer to what is now regarded as a single species, *Elymus trachycaulus*. Shading indicates names that represent, or were thought by their users to represent, awned and unawned variants of *A. parishii*. Names in bold-face represent basionyms of later names in that column. *Agropyron pauciflorum* and *Elymus pauciflorus* are both illegitimate as names for *E. trachycaulus* because each had been used for another taxon prior to being applied to elements of *E. trachycaulus*.

| Author | Year | | | | | | |
|-----------------------|------|--------------------------|---|---|--|--|--|
| Schweinitz | 1824 | | <i>Triticum pauciflorum</i> | | | | |
| Link | 1833 | | | <i>Triticum trachycaulon</i> | <i>Triticum subsecundum</i> | | |
| Vasey | 1885 | <i>Agropyron tenerum</i> | | | | | |
| Scribner & J.G. Smith | 1897 | | | | | <i>Agropyron parishii</i> var. <i>laeve</i> | <i>Agropyron parishii</i> var. <i>parishii</i> |
| Hitchcock | 1912 | <i>Agropyron tenerum</i> | | | | <i>Agropyron laeve</i> | <i>Agropyron parishii</i> |
| Malte | 1932 | | | <i>Agropyron trachycaulum</i> | | | |
| Hitchcock | 1934 | | | | <i>Agropyron subsecundum</i> | | |
| Hitchcock | 1935 | | <i>Agropyron pauciflorum</i> | | | <i>Agropyron parishii</i> var. <i>laeve</i> | <i>Agropyron parishii</i> var. <i>parishii</i> |
| Gould | 1947 | | <i>Elymus pauciflorus</i> | | <i>Elymus pauciflorus</i> subsp. <i>subsecundus</i> | <i>Elymus pauciflorus</i> subsp. <i>laevis</i> | <i>Elymus stebbinsi</i> |
| Shinners | 1954 | | | <i>Elymus trachycaulus</i> | | | |
| Hoover | 1966 | | | | | <i>Elymus laevis</i> | <i>Elymus laevis</i> |
| A. Löve & D. Löve | 1984 | | <i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i> | <i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i> | <i>Elymus trachycaulus</i> subsp. <i>subsecundus</i> | [Not mentioned] | |
| Barkworth | 1993 | | <i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i> | <i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i> | <i>Elymus trachycaulus</i> subsp. <i>subsecundus</i> | <i>Elymus trachycaulus</i> subsp. <i>subsecundus</i> | <i>Elymus stebbinsi</i> |
| Barkworth | 1998 | | <i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i> | <i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i> | <i>Elymus trachycaulus</i> subsp. <i>subsecundus</i> | <i>Elymus trachycaulus</i> subsp. <i>subsecundus</i> | <i>Elymus stebbinsi</i> subsp. <i>sepi-trionalis</i> |

Table 2. Characteristics of *Elymus glaucus*, *E. stebbinsii* subsp. *stebbinsii*, and *E. stebbinsii* subsp. *septentrionalis* based on specimens included in this study. Values shown for continuous characters are minimum, mean, maximum of typical specimens, with minimum and maximum for depauperate specimens of the two subspecies of *E. stebbinsii* shown in parentheses. The data for *Elymus glaucus* reflect a bias inherent in the loan request which was for specimens that had been identified as *E. stebbinsii*.

| Character Description | <i>Elymus glaucus</i> | <i>Elymus stebbinsii</i> subsp. <i>stebbinsii</i> | <i>Elymus stebbinsii</i> subsp. <i>septentrionalis</i> |
|---|--|--|--|
| 1 Thickness of the lowest internode and sheaths | 0.7-1.71-2.5 | 1.2-1.99-2.8 (1.0-1.9) | 1.8-2.60-3.6 (1.4-2.9) |
| 2 Lowest visible node | 28 glabrous, 8 pubescent | 8 glabrous, 9 pubescent (5 glabrous, 1 pubescent) | 36 glabrous, 2 pubescent (all 7 glabrous) |
| 3 Lower leaf sheaths | 34 glabrous, 2 pubescent | 16 glabrous, 1 pubescent (all glabrous) | 37 glabrous, 1 pubescent (all 7 glabrous) |
| 4 Lower leaf sheath margins | 34 glabrous, 2 ciliate | 12 glabrous, 5 ciliate (5 glabrous, 1 ciliate) | 34 glabrous, 4 ciliate (all 7 glabrous) |
| 5 Auricle length (mm) | 0.3-1.26-2.8 | 0.2-1.43-2.8 (0.2-2.8) | 0.5-1.31-2.1 (0.4-2.0) |
| 6 Ligule length (basal leaf) (mm) | 0.3-0.87-1.8 | 0.5-1.99-5.0 (0.2-2.1) | 0.2-0.68-1.3 (0.5-0.8) |
| 7 Blade width (widest available) (mm) | 2.2-4.05-6.0 | 2.6-4.64-8.0 (2.3-3.7) | 2.2-4.33-6.5 (3.0-5.5) |
| 8 Blade adaxial pubescence | 9 glabrous, 11 scabrous, 7 slightly to moderately pilose, 8 densely pilose | 3 glabrous, 1 scabrous, 3 slightly to moderately pilose, 10 densely pilose | 6 glabrous, 12 scabrous, 15 slightly to moderately pilose, 12 densely pilose |
| 9 Rachis internode length (average of 3 middle internodes) (mm) | 7.3-11.00-16.5 | 16.3-21.15-27.0 (9.7-15.0) | 9.5-14.77-20.3 (10.3-15.7) |
| 10 Maximum number of spikelets per node | 1-1.25-2 | 1 | 1 |
| 11 Spikelet length (longest available) (mm) | 11.2-15.13-20.0 | 17.5-22.25-29.0 (12.1-16.0) | 13.0-16.74-22.0 (11-19) |
| 12 Maximum number of florets per spikelet | 3-4.5-6 | 5-7.0-9 (3-5) | 4-4.80-6 (3-6) |
| 13 First glume length (mm) | 6.0-11.12-20.0 | 6.0-10.82-15 (4.1-8.5) | 7.3-10.08-12.8 (6.0-11.0) |
| 14 Glume apex shape | 35 acuminate to strongly tapering | 13 acute, 4 acuminate | 40 acute, 5 acuminate |
| 15 Second glume length (mm) | 6.0-11.78-16.0 | 7.0-11.70-15.0 (6.0-9.5) | 7.9-11.13-13.8 (8.0-12.0) |
| 16 First lemma length (mm) | 8.0-10.79-13.0 | 9.5-12.23-14.5 (9.4-12.0) | 9.0-11.68-15.0 (9.5-11.3) |
| 17 First lemma awn length (mm) | 2.0-12.52-26.0 | 1.5-5.75-11.6 (3.0-7.0) | 8.0-16.15-25.0 (6.5-21.0) |
| 18 First palea length (mm) | 8.7-9.85-12.0 | 9.4-11.50-13.5 (8.2-11.5) | 98.50-10.81-13.0 (8.8-10.3) |
| 19 Anther length (mm) | 2.0-3.45-4.6 | 4.6-5.64-7.0 (3.2-5.4) | 4.2-5.6-7.1 (4.1-6.0) |

There were several sets of duplicate specimens among those scored. These were deliberately kept in the analyses so as to provide a biological basis for evaluating the results of the numerical analyses.

The 19 characters scored included those mentioned by previous taxonomists as distinguishing the two taxa, plus some that my initial studies suggested might be of taxonomic value. Characters not available on a specimen were scored as missing. Only the continuous characters and floret number were used in the numerical analyses. The other characters were used to evaluate the groups suggested by these analyses and to assist in identifying specimens not included in the numerical analyses. Of the 148 specimens scored, 126 had data for all characters except floret number; 122 could be scored for all characters.

Four numerical procedures were used to explore the variation present: sequential agglomerative hierarchical nested cluster analysis (SAHN), principal component analysis (PCOMP), minimum spanning tree (MST), and discriminant analysis (DA). Principal component analysis was conducted on the correlation matrix. For MST and SAHN, the data were standardized by subtracting the mean and dividing by the standard deviation. Taxonomic distance (Sneath & Sokal 1973) was used as the distance measure.

Cluster analysis forces the OTUs into clusters. The taxonomic merit of these clusters can then be evaluated by examining whether they are supported by variation in characters not included in the analysis. Whenever feasible, different kinds of characters (*e.g.*, cytological, molecular) should be used in evaluating the predictive power of the clusters. Time and financial constraints limited me to characters evident on herbarium specimens.

Three clustering algorithms were employed: single linkage, complete linkage, and unweighted pair group mathematical average (UPGMA) (Sneath & Sokal 1973). Only UPGMA consistently placed members of duplicate OTU sets within the same major cluster; consequently only UPGMA results are presented.

Principal component analysis does not require the *a priori* assignment of OTUs to groups, but seeks to minimize the number of axes needed to portray the variation within a data set. It accomplishes this by constructing axes for a hyperdimensional space from linear combinations of the original data. The distribution of the OTUs along the first principal component (axis) accounts for as much of the variation in the original data set as possible, their distribution along the second principal component accounts for as much of the remaining variation as possible, with subsequent components doing the same for the ever-decreasing amount of variation left. The number of principal components needed to account for all the variation depends on the amount of correlation in the original data, fewer components being required if the data are highly correlated.

Although principal component analysis does not identify groups among the data, OTUs with different character correlations will be concentrated in different portions of the principal component space. A set of OTUs with similar character correlations will form a "cloud" in the character space. The taxonomic merit of such a set can then be evaluated by determining whether it is supported by the pattern of variation in

characters not used in the analysis (Davis & Heywood 1963). Because only the projection of the OTUs onto the first three principal components was examined, MST was used to determine the closest neighbor of each OTU and these connections were superimposed on the PCOMP projection.

Discriminant analysis seeks to maximize the separation among pre-defined groups of OTUs based on linear combinations of the original data. These linear combinations, or functions, are then applied to each OTU and its group membership assessed. If the functions place the OTU closer to the centroid of a group other than its own group, that OTU is flagged as misclassified and the group with the closest centroid identified.

Because I had no independent criteria for assigning the OTUs to groups, I used the major clusters obtained from UPGMA cluster analysis as the initial groups. The membership of these groups was then modified to reflect the classification suggested by the first DA. This procedure was repeated until the discriminant functions placed all the OTUs in the group to which they had been assigned.

I then reevaluated the resulting groups of OTUs in terms of characters not used in the analyses. This resulted in the reclassification of a few OTUs. The data from these groups were then used to evaluate the specimens not included in the numerical analyses and a preliminary taxonomic treatment developed. After further review of the specimens, I examined the geographic and ecological distribution of the taxa that seemed to merit recognition, and summarized the morphological data for the three that were well represented in the study.

EXCEL (Microsoft 1997) was used to record the data and calculate univariate statistics. NTSYS (Rohlf 1993) was used for PCOMP, SAHN, and MST, and SYSTAT (SPSS 1997) for the discriminant analyses. To plot distributions, the latitude and longitude for each collection site represented was estimated using StreetAtlas (DeLorme 1997), Geographic Names Information System (U.S. Geological Survey 1993), or Wefald's (1995) program for converting township, range, and section data to latitude and longitude. Distribution maps were produced using Atlas Graphics version 2.1 (Strategic Mapping 1993).

RESULTS

CLUSTER ANALYSIS. Cluster analysis, using UPGMA, resulted in the formation of four major clusters (Figure 1) among the OTUs. The cluster containing the holotype of *Elymus stebbinsii* is labeled Sb, that containing what is designated below as the holotype of *E. stebbinsii* subsp. *septentrionalis* is labeled Sp. The other two clusters, A and B, consisted primarily of OTUs that belonged to the single spikelet variant of *E. glaucus*.

Groups A, B, and Sp were somewhat unstable. Measuring a different spikelet on a specimen sometimes moved a specimen from one cluster to another and the addition of a few specimens with missing anthers also altered the order in which the clusters linked together. Most of the movement involved groups A and B.

Surveying the specimens in each cluster, including looking at the characters not used in the analyses, convinced me that the clusters were taxonomically interesting entities, but that they were not identical with good taxa.

PRINCIPAL COMPONENT ANALYSIS. The first three principal components accounted for 37.1%, 17.1%, and 11.1%, respectively, of the total variance. Spikelet and floret characters contributed most to the first and second axes; basal culm diameter was the largest contributor to the third axis (Table 3).

Table 3. Coefficients of the five most significant characters in determining the location of OTUs on the first three principal components.

| | Component 1 | Component 2 | Component 3 |
|---------------------|------------------------------|---------------------------------|----------------------------------|
| Largest contributor | Lemma length (0.8065) | Awn length (-0.6432) | Culm basal diameter (-0.6646) |
| Second contributor | Spikelet length (0.8952) | Second glume length (0.6070) | Anther length (0.6117) |
| Third contributor | Floret number (0.7740) | First glume length (0.6040) | First glume length (0.4240) |
| Fourth contributor | Rachis internode (0.7177) | Ligule length (0.5300) | Second glume (0.3633) |
| Fifth contributor | Second glume (0.6259) | Blade width (0.4577) | Awn length (0.3333) |

The projection of the OTUs onto the first three components (Figure 2) revealed no strongly defined groups among the OTUs. The Sb group [using labels from the cluster analysis] was the most distinct, but its intra-group distances were also relatively large. The other three groups occupied basically different, but contiguous, portions of the principal component space, with the Sp group between groups A and B. Minimum spanning tree links provide an indication of the overlap among the groups. Ideally, the maximum number of intergroup links would be two per group, with two of the groups having only a single intergroup link, *i.e.*, 6 links for 4 groups. There were 21 intergroup links among the OTUs in this study. Group Sb had 5 (3 to Sp, 2 to A); group Sp had 11 (6 to B, 3 to Sb, and 2 to A); group A had 12 (8 to B, 2 to Sp, and 2 to Sb), and group B had 14 (8 to A, 6 to Sp).

DISCRIMINANT ANALYSIS. It was hard to determine, from looking at the specimens, which characteristics contributed most to the distinction between groups A and B, but comparison of the means for each cluster suggested that awn length was a major factor. For this reason, and because of the instability of the clusters, I decided to conduct two series of discriminant analyses, one in which A and B were considered as separate groups and one in which they were combined into a single group.

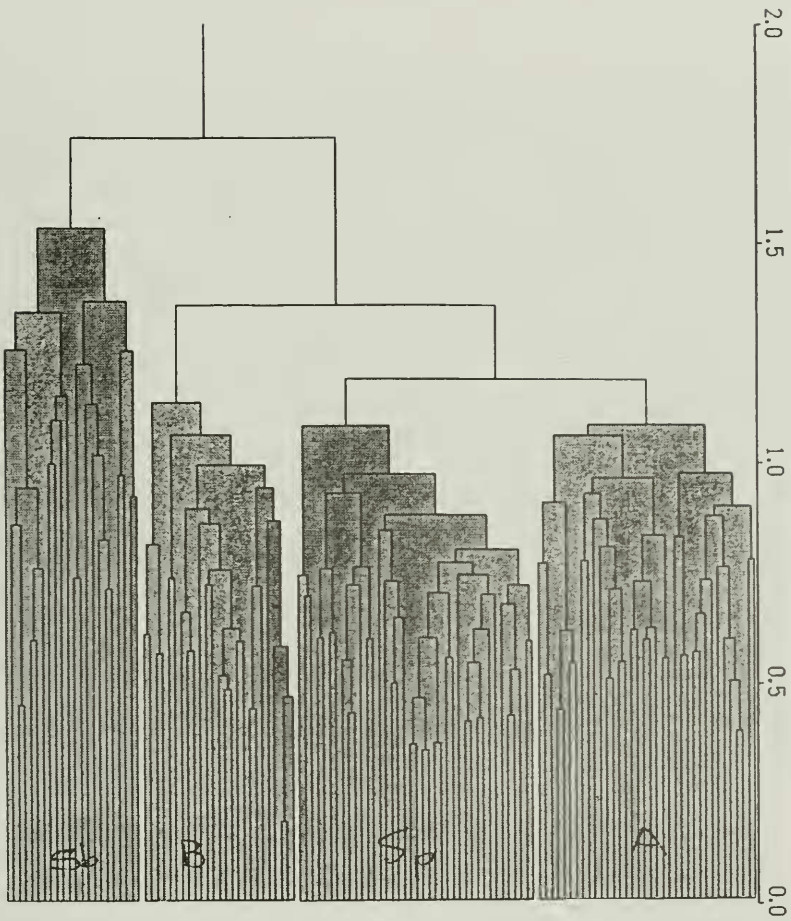


Figure 1. Results of UPGMA cluster analysis. The four major clusters are, from left to right, Sb, B, Sp, and A.

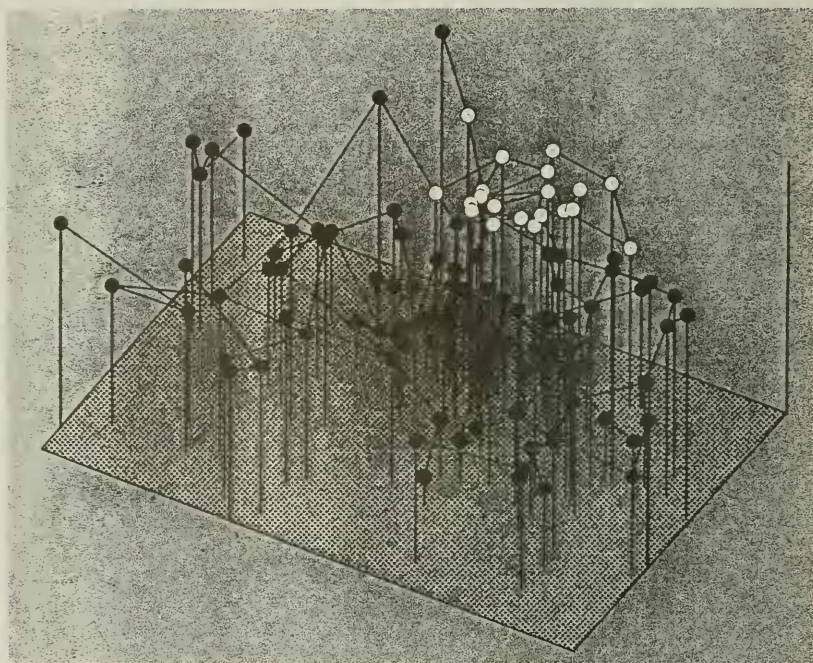


Figure 2. Projection of the OTUs onto the first three principal components. White - cluster A, light gray - cluster Sb, dark gray - cluster B, black - cluster Sp. Lines show links formed by Minimum Spanning Tree. The longest axis is the first axis, the vertical axis is the third axis.

Both series of DA disagreed with the cluster analysis in the placement of a few OTUs, but neither series considered any of the Sb group OTUs misclassified. In the 4-group analysis, 2 OTUs had to be reassigned before discriminant functions were generated that considered all OTUs correctly assigned, one from group Sp to group A, the other from cluster A to cluster B. Even then, jackknife analysis suggested that eight OTUs (9% of those in the analysis) were misclassified. With three groups, seven specimens had to be reassigned before the classification matrix showed no misclassifications, six from group A+B to group Sp, and one from group Sp to group A+B, the same OTU as was moved from group Sp to group A in the four-group analysis. Jackknife analysis resulted in a 5% misclassification rate.

Both series of discriminant analyses placed group Sp closer to the groups A and B (4-group series) or group A+B (3 group series) than to group Sb. Thinking that might be a reflection of awn length, I ran a 3-group analysis excluding the awn length character. This moved group Sp closer to group Sb, but it remained closest to the A+B group.

GROUP EVALUATION. To further evaluate the groups suggested by the numerical analyses, I obtained summary statistics for the four major groups, after modifying them to reflect the results of the discriminant analyses. The OTU that both series of discriminant analyses suggested should be reassigned was placed in the suggested group. The other supposedly misclassified OTUs were left in the group suggested by the cluster analyses.

Group Sb had more florets per spikelet, and longer ligules, rachis internodes, and spikelets, but shorter awns, than the other three groups. It resembled group Sp, and differed from groups A and B, in having longer anthers and somewhat longer florets. Group Sp differed from all other groups in having, on average, longer awns and thicker culms, but it overlapped the other groups in its extreme values. It differed from group Sb and resembled groups A and B in having relatively few florets per spikelet.

Group A differed from group B primarily in the longer length of its awns, glumes, and lemmas. The greatest difference between the two was in awn length, group A having longer awns. Group B also contained a number of OTUs with glumes that were unusually short relative to the first lemma.

QUALITATIVE CHARACTERS. Qualitative characters and the maximum number of spikelets per node were not included in the numerical analyses. Most were of little or no taxonomic value. Pubescent culm nodes were found on 50% of the OTUs in group Sb, but occurred, albeit less frequently, in the other three groups. Pubescent sheaths and ciliate sheath margins were uncommon in all groups. Adaxial blade vestiture varied from glabrous and smooth, through scabridulous to scabrous, to scabrous with some short pilose hairs, to densely pilose, but I could find no relationship between the vestiture and other characters.

Two characters, maximum number of spikelets per node and glume apex shape, were more interesting. Two spikelets per node were more common in groups A and B than groups Sb and Sp, although they were not common in any group. This last was partly an artifact of the loan request which specified taxa specimens identified as

belonging to taxa that customarily have solitary spikelets. Glume apex shape was the most promising taxonomic character. All OTUs in group A had tapering or acuminate glume apices, as did 40% of those in group B and 21% of those in group Sb, but none of those in group Sp. In looking more closely at the variation in this character, I noted that the glumes of OTUs in groups Sp and Sb were often completely smooth or scabridulous only on the distal portion of the midvein. Glumes of groups A and B specimens were often scabridulous over more of the midvein as well as over other veins. In addition, the base of the glumes in groups Sp and Sb were more apt to have evident ridges over the veins whereas specimens in groups A and B usually had smooth glume bases. There were, however, exceptions in both directions.

Another character that tended to distinguish groups Sb and Sp from groups A and B, the shape of the palea apex, became apparent during the course of this study. In OTUs of groups Sb and Sp, the palea veins scarcely converged and the end of the intercostal tissue was truncate. In most OTUs of groups A and B the veins converged more strongly and the intercostal tissue had a V-shaped notch, making the palea apices look acute and bifid. Examination of specimens of *Elymus glaucus* and *E. trachycaulus* in UTC from Utah and Idaho suggested that converging paleal keels and a slightly notched palea apex are common in these two species. According to this criterion, most specimens referable to groups A and B belonged to *E. glaucus* or *E. trachycaulus*, but some belonged to group Sb or Sp. Unfortunately, there is some variation in the palea character within a plant. Moreover, Connor (1994) found that, in New Zealand species of *Elymus*, the blunt and truncate to slightly retuse palea apex appears to be a dominant single gene character, suggesting that this palea character should be used with caution.

I used the results of the various analyses to develop tentative descriptions and diagnoses for four taxa, corresponding to the four groups, and then reviewed all the specimens available to me to determine in which group I would place them. In doing so, I was aware that the characters analyzed had been selected for their ability to distinguish specimens of *Elymus stebbinsii* from other taxa with which it had been confused. There was no *a priori* reason why groups A and B should be taxonomically significant or homogeneous.

The review showed that all the specimens in group Sb were referable to Scribner & Smith's *Agropyron parishii* var. *parishii*, but it did not include some of the less robust specimens that I would have included in that taxon. The specimens occur primarily in the Coast Ranges, the Tehachapi Mountains, and the Transverse Ranges.

Group Sp consisted of plants that differed from group Sb plants primarily in having longer awns and fewer florets (on average). They also had a somewhat different geographic distribution, occurring primarily on the west slopes of the Sierra Nevada and in the southern Cascade Mountains (Hunt 1974), often in yellow pine forests. As with group Sb, some less robust specimens that I would have assigned to group Sp were placed in groups A and B by the numerical analyses. I concluded that the specimens in group Sp should be regarded as part of *Elymus stebbinsii* but that they should be recognized as representing a distinct subspecies because of their morphological and distributional differences from specimens in the group that included the holotype of *E. stebbinsii*.

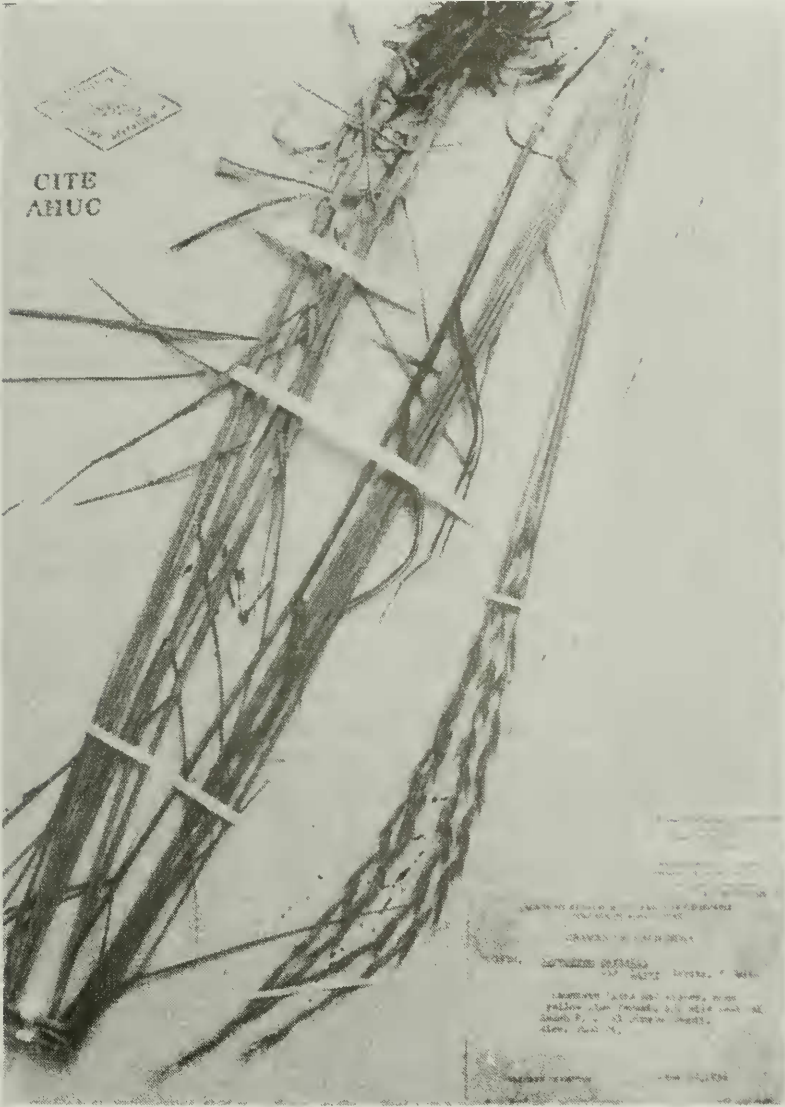


Figure 3. Holotype of *Elymus stebbinsii* subsp. *septentrionalis*. Note the robust culm and widely spaced spikelets.

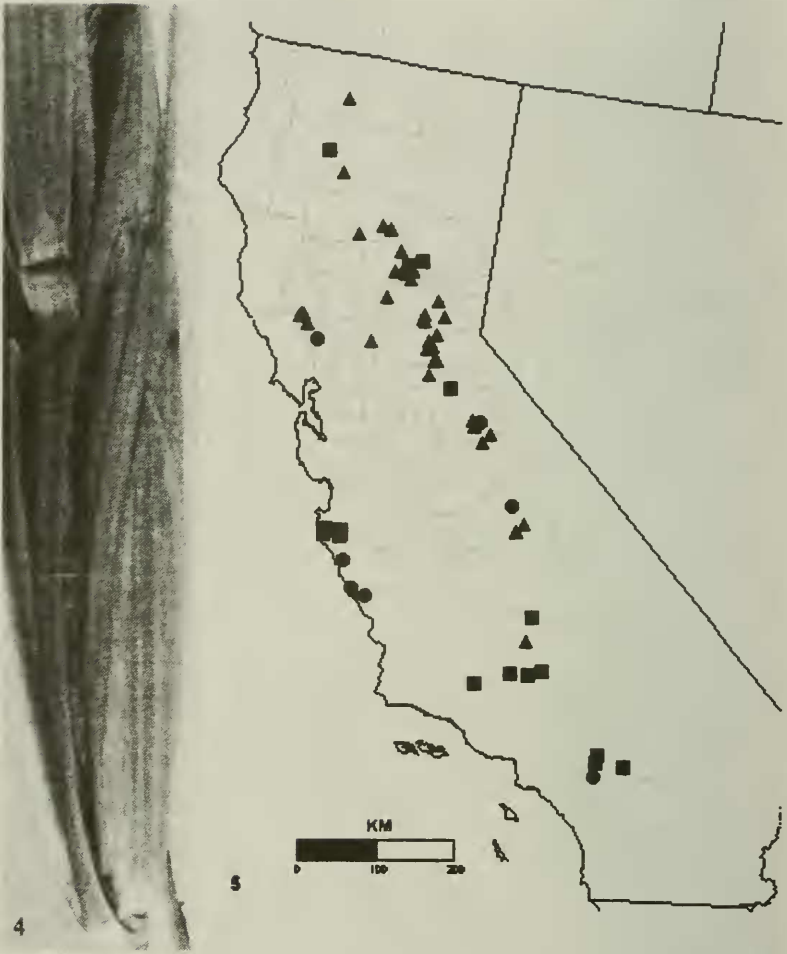


Figure 4. Spikelet from holotype, showing glumes and palea apex.

Figure 5. Distribution map of *Elymus stebbinsii*. Squares - specimens for which the subspecies could not be determined, circles - subsp. *stebbinsii*, triangles - subsp. *septentrionalis*.

Most group A and B OTUs belonged to *Elymus glaucus*, but both groups included some depauperate specimens of the two *E. stebbinsii* subspecies. These depauperate specimens had the long anthers and acute, relatively smooth glumes characteristic of *E. stebbinsii*, but had thinner culms, shorter spikelets and spikelet parts, and proportionately shorter glumes, than typical members of the species. Most were relatively long-awned, but a few had short awns. Their geographic distribution mimicked that of the two subspecies of *E. stebbinsii*.

I re-analyzed the data after removing the specimens that I was confident did not correspond to either variety of *Agropyron parishii*. The results were not encouraging. Cluster analysis identified three major clusters. Two of these corresponded in general to groups Sb and Sp, but the third cluster contained some of the OTUs that had previously been placed in group Sb or Sp. Because there was no hint that further analyses of the same specimens would clarify the taxonomy of the specimens involved, I halted the study at this stage.

CONCLUSIONS

Completing a taxonomic study of morphologically similar taxa solely on the basis of herbarium specimens is frustrating. One cannot assess populational variation, nor the extent to which a taxon's morphology may be modified by various kinds of stress. My original goal was simply to determine whether there was a taxon corresponding to Scribner & Smith's description of *Agropyron parishii* var. *laeve* but, to address it, it became necessary to re-evaluate the morphological limits of *Elymus glaucus* and *E. trachycaulus*.

The results obtained in this study support recognition of two taxa within *Elymus stebbinsii*. One, corresponding to group Sb, consists of shortly awned plants with large spikelets having 6-9 florets per spikelet and occurs in the Coast and Transverse Ranges. The other, corresponding to group Sp, is a longer-awned taxon with somewhat fewer florets per spikelet that occurs to the north and east of the Great Central Valley. It is possible that the long-awned taxon corresponds to Scribner & Smith's var. *laeve* taxon and that the choice of a type was simply unfortunate, but this cannot be determined with certainty. They (Scribner & Smith 1897) did not include anther length, the most consistent reliable character for distinguishing between *E. trachycaulus* and *E. stebbinsii*, in their description of *Agropyron parishii*, nor did they provide distributional information for the taxon. Nevertheless, Gould having recognized that the holotype of *A. parishii* var. *laeve* belongs in *E. trachycaulus*, a new epithet must be found for the long-awned taxon in *E. stebbinsii*.

Although the numerical analyses place the long-awned taxon closer to *Elymus glaucus* and *E. trachycaulus* than *Agropyron parishii* var. *parishii*, the shape of its glumes and palea suggest that it is genetically closer to var. *parishii* than either of the other two taxa. This is confirmed by its similarity to var. *parishii* in the distinctive characters of typical members of that taxon, i.e., the robust, somewhat decumbent culms, the widely spaced spikelets, and long anthers. Because the long-awned taxon tends to be geographically distinct from var. *parishii* (Figure 3), I propose that it be

recognized as *E. stebbinsii* subsp. *septentrionalis*, thereby automatically creating the name *E. stebbinsii* subsp. *stebbinsii* for *A. parishii* var. *parishii*. No specimens of either subspecies of *E. stebbinsii* were found from San Diego County, location of the type of *A. parishii* var. *laeve*.

Elymus stebbinsii Gould subsp. *septentrionalis* Barkworth, subsp. nov.
HOLOTYPE: U.S.A. California: El Dorado County, 0.5 miles west of Omo Ranch Post Office, 22 June 1956, *Beecher Crampton 3598* (AHUC 22602 [Figures 3,4]).

Differt a subsp. *stebbinsii* arista lemmatis longiore et nodo infirmo persaepe glabro.

Gramen perennis. Culmi laxe fasciculati, erecti vel basi decumbentibus, 70-130 cm altus, internodio infirmo (1.4)1.7-3.6 mm crasso; nodi persaepe glabro. Foliorum vaginae persaepe glabrae, margines fauci ciliati; auriculae 0.4-2.6 mm longae, falcatae; ligulae 0.25-1.25 mm, truncatae, ciliatae; laminae 2.2-6.5 mm latae, glabrae, scabrae, vel pilosae. Inflorescentia spica una spicula in quoque nodo; internodia 9.5-20.3 mm; spiculae (11)13-22 mm longa, flosculi 4-6; gluma inferior (6.0)7.7-12.8 mm, acuta, gluma superior parum longior; lemma infima 9.5-15.0 mm, terminans arista (6.5)11-25 mm, lemmae longior vel paulo brevioribus; palea lemmae paulo brevioribus; antherae 4.1-7.1 mm longae.

Paratypes: U.S.A. California: Butte County, along Big Bar Road, about 1 mile south-west of Coyote Gap, 8 July 1987, *Lowell Ahart 5805* (CHSC 42952); El Dorado County, 1.8 miles west of Omo Ranch Post Office, 22 June 1956, *Beecher Crampton 3590* (UC 1040715); Lake County, 1 mile east of Loch Lomond, 26 June 1956, *Beecher Crampton 3626* (AHUC 22604); Placer County, Shirttail Canyon, 6.5 miles west of Iowa Hill, 15 June 1955, *Beecher Crampton 2895* (AHUC 21154).

Differing from subsp. *stebbinsii* in its longer lemma awns and almost always glabrous lowermost culm node.

Perennial grass. Culms loosely clustered, erect or decumbent at the base, 70-130 cm tall; lower internodes (1.4)1.7-3.6 mm thick, the lowermost node almost always glabrous. Leaf sheaths almost always glabrous, the margins of the throat ciliate; auricles 0.4-2.6 mm long, falcate; ligules 0.25-1.25 mm, truncate, ciliate; blades 2.2-6.5 mm wide, glabrous, scabrous, or pilose. Inflorescence a spike with one spikelet per node; middle internodes 9.5-20.3 mm; spikelets (11)13-22 mm long, with 4-6 florets. Lower glume (6.0)7.7-12.8 mm long, acute; upper glume slightly longer; lowest lemma 9.5-15.0 mm, terminating in an awn (6.5)11-25 mm long, longer or slightly shorter than the lemma; palea slightly shorter than the lemma; anthers 4.1-7.1 mm long.

Typical members of the two varieties of *Elymus stebbinsii* are robust plants with thick, decumbent culms. Among the specimens studied, however, there were several slender, delicate plants that had the distant spikelets, truncate palea apices, and acute glumes characteristic of *E. stebbinsii*, but the glumes that tended to be shorter in proportion to the first lemma than those of typical specimens (most fell into group B). I considered recognizing them as a distinct taxon but decided against doing so because

there were both awned and unawned specimens present and the distribution of these mimicked that of the robust specimens. In addition, even when the non-*stebbinsii* OTUs were removed from the data set, the delicate specimens did not form a distinct cluster, but occurred within the Sb and Sp clusters. I strongly recommend further study of such plants. They may be nothing more than depauperate plants, but the lack of continuity between them and typical representatives of the two subspecies is disconcerting.

Representatives of the short-glumed variant include Kern County, swale at head of Mill Creek, 27 July 1965, *Ernest C. Twisselmann 11239* (AHUC 32447); Mariposa County, above Wawona Road Tunnel, 17 July 1936, *Lyman Benson 7893* (POM 295836); Placer County, along southeast bank of American River, 1.5 miles northeast of bridge on Colfax-Iowa Road, 22 June 1952, *G.L. Stebbins, Jr. 5102* (CAS 376178); Plumas County, near Lewisia rock in Feather River Canyon, 12 June 1968, *John Thomas Howell 44561* and *Gordon H. True* (CAS 633387); Siskiyou County, canyon north of Willow Creek, 5 miles west of Gazelle, 31 May 1942, *A.A. Beetle 3406* and *G.L. Stebbins, Jr.* (AHUC 7519); Yuba County, about 2 miles east of Challenge, 25 June 1979, *Lowell Ahart 1946*.

The two subspecies of *Elymus stebbinsii* are generally geographically separated but *Ahart 5887* (CAS 916837, CHSC 43290), from Butte County, was exceptional in having the characteristics of subsp. *stebbinsii* despite coming from northeastern California. Illustrations of both subspecies of will be included in the *Manual of Grasses for the Continental United States and Canada* (Barkworth *et al.*, in prep.).

Glume shape is the best character for distinguishing *Elymus stebbinsii* from specimens of *E. glaucus* with solitary spikelets and long anthers. Palea shape and basal culm thickness also appear to be helpful (Table 2). A few specimens suggest that the two species may form partially fertile hybrids (*e.g.*, San Antonio Mountains, Browns Flat, dry open ground under pine, 1 July 1917, *I.M. Johnston 1518* [DS 83847]; Tuolumne County; Strawberry, 5300 ft, June 1951, *A. Haig s.n.* [AHUC 14340]; Kern County, East fork of Upper San Emigdio Canyon, Douglas oak-pinyon association, 22 June 1961, *Ernest C. Twisselmann 6284* [CAS 523141]).

Distinguishing *Elymus trachycaulus* from *E. stebbinsii* does not present a problem if anthers are present. Distinguishing it from *E. glaucus* is often harder, even if anthers are present. I wish I could state that I now know how to separate herbarium specimens of the two taxa with confidence. I cannot. Some specimens are easy to place in one species or the other, but there are a disturbingly large number with solitary spikelets that I find extremely hard to identify with any degree of confidence.

There were two specimens examined during this study that were particularly interesting. I include information about them here in the hope that it will stimulate others to examine them, and the sites from which they were obtained, in greater detail. One such specimen was El Dorado County, 2.6 mi southeast of Placerville, roadcut, shaded slope forested by yellow pine and oak, June 22, 1956, *Beecher Crampton 3617* (AHUC 22601). This was a robust specimen (culm 155 cm tall, basal diameter 3.1 mm) with well-spaced, long-awned spikelets (internodes 14 mm, spikelets 15 mm, awns to 18 mm), truncate paleas, and long (5.7 mm) anthers. The distinctive features were its long spikes (around 25 cm) and short (about 8 mm), stiff, almost truncate glumes reminiscent of *Thinopyrum intermedium*. Of the Triticeae with which

I am acquainted, it is closest to *E. stebbinsii* subsp. *septentrionalis*, but it is an unusual representative of that taxon. Another interesting specimen was Monterey County, Pico Blanco, May-June 1901, *J. Burt Davy 7364* (UC 607791). It belongs in *E. stebbinsii* subsp. *stebbinsii*, but it has narrow, convolute leaves that distinguished it from all other specimens of the taxon.

Table 2 summarizes data obtained for *Elymus stebbinsii* and *E. glaucus* obtained in this study. The data for *E. glaucus* came from a very biased sample. All the specimens involved came from California although the species extends north to Alaska and east to the Central Plains. In addition, they were included in the study because they had been identified as *E. stebbinsii*. This criterion biased the sample towards plants with large, solitary spikelets and longer anthers than is typical for the species. No data are presented for *E. trachycaulus* because very few were included in the numerical portion of the study. The key to Californian species of *Elymus* that follows reflects the results of this study and the decision to include quackgrass in *Elymus* as *E. repens*.

KEY TO THE CALIFORNIAN SPECIES OF *ELYMUS*

1. Glumes absent; spikelets usually 3-4 per node.....*E. californicus*
- 1' Glumes present, lanceolate to setaceous; spikelets usually 1-3(4) per node.
 2. Rachis disarticulating at maturity; glumes narrow to setaceous, terminating in an awn 25-100 mm long.
 3. Glumes 3-many cleft; auricles conspicuous, usually around 1 mm long.....*E. multisetus*
 - 3' Glumes entire or 2-cleft, rarely 3-cleft with 2 short lateral awns; auricles less than 1 mm or wanting.....*E. elymoides*
 4. Spikelets 3 at each node, only the central spikelet with fertile florets.....*E. elymoides* subsp. *hordeoides*
 - 4' Spikelets 2 at each node or, if more, the lateral spikelets with one or more fertile florets.
 5. All florets in the spikelet similar... *E. elymoides* subsp. *longifolius*
 - 5' First floret of some lower spikelets glume-like, the spikelets consequently appearing to have 3 glumes.
 6. At least one glume at the lower nodes 2-cleft.....*E. elymoides* subsp. *elymoides*
 - 6' All glumes entire..... *E. elymoides* subsp. *californicus*
 - 2' Rachis not disarticulating at maturity except in *E. scribneri*; glumes lanceolate, sometimes narrowly so, unawned or the awn less than 10 mm long.
 7. Spikelets 2 or more at most nodes.
 8. Inflorescence nodding; glumes curving at the base, exposing the base of the first floret; lemma awns arcuately diverging.....*E. canadensis*
 - 8' Inflorescence erect; glumes straight at the base, concealing the base of the first floret.....*E. glaucus*
 9. Lemma awns less than 9 mm long.... *E. glaucus* subsp. *virescens*
 - 9' Lemma awns 10-30 mm long.

- 10. Lower leaf sheaths smooth or scabrous,
not pubescent..... *E. glaucus* subsp. *glaucus*
- 10' Lower leaf sheaths pubescent. *E. glaucus* subsp. *jepsonii*
- 7' Spikelets solitary at all or most nodes.
- 11. Plants strongly rhizomatous; anthers 3-6 mm long.
- 12. Glumes rounded at the base, strongly keeled above, the
midveins smooth below and scabrous above..... *E. repens*
- 12' Glumes more or less rounded throughout their length,
the midvein evenly scabrous from the base or
less so above..... *E. lanceolatus*
- 11' Plants caespitose, not rhizomatous; anthers 1-5 mm long.
- 13. Lemmas with arcuately diverging awns.
- 14. Inflorescence drooping; plants not subalpine or
alpine (doubtfully present in California)..... *E. arizonicus*
- 14' Inflorescence straight; plants of subalpine and alpine
habitats.
- 15. Rachis internodes 8-10 mm; rachis not
disarticulating at maturity..... *E. sierrae*
- 15' Rachis internodes 3.5-8.0 mm; rachis
disarticulating at maturity..... *E. scribneri*
- 13' Lemmas unawned or the awn straight.
- 16. Glumes acute, unawned; rachis internodes
16-21 mm; anthers 4.2-7.2 mm..... *E. stebbinsii*
- 17. Lemma awns 1.5-11.5 mm; florets 5-9
per spikelet; leaf sheaths often
pubescent..... *E. stebbinsii* subsp. *stebbinsii*
- 17' Lemma awns (8) 12-25 mm long; florets
4-6 per spikelet; leaf sheaths occasionally
pubescent..... *E. stebbinsii* subsp. *septentrionalis*
- 16' Glumes acute or tapering to acuminate or awned;
rachis internodes 4.0-16.5 mm; anthers 0.8-4.6
mm (anthers short if glumes acute).
- 18. Glumes acuminate, often awned, the veins
usually equally scabridulous throughout;
anthers 2.0-4.6 mm (see above for varieties).... *E. glaucus*
- 18' Glumes acute to acuminate, the midvein
often more scabridulous than the others;
anthers 0.8-2.5 mm..... *E. trachycaulus*
- 19. Lemma awns longer than the body,
8-30 mm. *E. trachycaulus* subsp. *subsecundus*
- 19' Lemma awns shorter than the body,
up to 7 mm. *E. trachycaulus* subsp. *trachycaulus*

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LITERATURE CITED

- Abrams, L. 1940. *Illustrated Flora of the Pacific States*. Stanford University Press, Stanford, California.
- Barkworth, M.E. 1993. *Elymus*. Pp. 1253-1256 in J.C. Hickman (Ed.), *The Jepson Manual: Higher Plants of California*. University of California Press, Berkeley, California.
- Barkworth, M.E. 1996. The *Elymus trachycaulus* complex in North America: many questions, few answers. Pp. 189-194 in Wang, R.R.-C., K.B. Jensen, & C. Jauss (Eds.), Proc. Second International Triticeae Symposium, Forage and Range Laboratory, U.S.D.A.-A.R.S., Logan, Utah.
- Connor, H.E. 1994. Indigenous New Zealand Triticeae: Gramineae. New Zealand J. Bot. 32:125-154.
- Davis, P.H. & V.H. Heywood. 1963. *Principles of Angiosperm Taxonomy*. D. Van Nostrand Company, Inc., Princeton, New Jersey.
- DeLorme. 1997. Street Atlas USA, version 5.0. DeLorme Mapping, Freeport, Maine.
- Dremann, C. 1995. *Bromus carinatus* and *Elymus glaucus* storage, longevity, genetic changes, and ecotypical variations. Grasslands 5:2-5.
- Gould, F.W. 1947. Nomenclatural changes in *Elymus* with a key to the Californian species. Madroño 9:120-128.
- Hall, H.M. 1902. A botanical survey of San Jacinto Mountain. Univ. Calif. Publ. Bot. 1:1-140.
- Hitchcock, A.S.. 1912. Gramineae. Pp. 82-189 in W.L. Jepson, *A Flora of California*, part 3. Associated Students Store, University of California, Berkeley, California.
- Hitchcock, A.S. 1935. *Manual of Grasses of the United States*. U.S.D.A. Misc. Publ. 200, Washington, D.C.
- Hitchcock, A.S. 1951. *Manual of Grasses of the United States*. Ed. 2, revised by A. Chase. U.S.D.A. Misc. Publ. No. 200, Washington, D.C.
- Holmgren, P.K., N.H. Holmgren, & L.C. Barnett. 1990. *Index Herbariorum*. Part 1: The herbaria of the world. Ed. 8. International Association for Plant Taxonomy, New York Botanical Garden, Bronx, New York.
- Hoover, R.F. 1966. Miscellaneous new names for California plants. Leaflet. W. Bot. 10:337-350.
- Hunt, C.B. 1974. *Natural Regions of the United States and Canada*. W.H. Freeman and Company, San Francisco, California.

- Lamarck, J.B.A.P.M. 1791. *Tableau Encyclopédique et Méthodique des Trois Règnes de la nature*. Chez Pancoucke, Paris, France.
- Microsoft Corporation. 1997. Excel 97. Microsoft Corporation, Bellevue, Washington.
- Munz, P.A. 1959. *A California Flora*. University of California Press, Berkeley, California.
- Rohlf, F.J. 1993. NTSYS-pc: numerical taxonomy and multivariate analysis system, version 1.80. Exeter Software, Setauket, New York.
- Scribner, F.L. & J.G. Smith. 1897. Native and introduced species of the genera *Hordeum* and *Agropyron*. U.S.D.A. Div. Agrostol. Rep. Agrostol. 4:23-36.
- Shinners, L.H. 1954. Notes on North Texas Grasses. *Rhodora* 56:25-44.
- Sneath, P.A. & R.R. Sokal. 1973. *Numerical Taxonomy: The Principles and Practice of Numerical Taxonomy*. W.H. Freeman, San Francisco, California.
- Snyder, L.A. 1950. Morphological variability and hybrid development in *Elymus glaucus*. *Amer. J. Bot.* 37:628-636.
- SPSS. 1997. SYSTAT 7.0 for Windows. SPSS Inc., Chicago, Illinois.
- Strategic Mapping. 1993. Atlas GIS, version 2.1. Strategic Mapping, Inc., Santa Clara, California.
- U.S. Geological Survey, National Mapping Division. = 1993. USGeoData: Geographic Names Information System, Earth Science Information Center, Reston, Virginia.
- Wefald, M. 1995. TRS2LL.EXE, a computer program for converting between township, range, section data and latitude and longitude in the western United States. Available by Email from stipoid@cc.usu.edu.